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Long-term winter-site fidelity in Song Sparrows (*Melospiza melodia*)

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Long-term winter-site fidelity in Song Sparrows *Melospiza melodia*

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Abstract

In migratory animals, the degree to which individuals return to the same wintering sites across multiple years can affect fitness and population dynamics, and thus has important implications for conservation. Despite this, long-term evaluations of wintering-site fidelity are rare for migratory birds: many populations are intensively studied on their breeding grounds but tracking the migratory movements of small birds once they leave the breeding grounds is challenging. To evaluate patterns of overwintering location and fidelity, we collected winter-grown claw tissue from 301 Song Sparrows (*Melospiza melodia*; 449 samples) captured in spring at their breeding grounds over six consecutive years and assessed stable hydrogen isotope ($\delta^2\text{H}_c$) values to determine within-individual repeatability and between-year variation in wintering latitudes. We also retrieved useable data from eight geolocators over two consecutive winters. Geolocator-derived wintering positions correlated with origins based on $\delta^2\text{H}_c$ values. Consistent with previous findings, male $\delta^2\text{H}_c$ values reflected more northerly wintering areas than those of females, indicating shorter latitudinal migration distances for males, but the magnitude of the sex difference varied across years. The distribution of wintering latitudes was generally consistent among years, except for the 2015 – 2016 winter that had unusually negative $\delta^2\text{H}_c$ values. Values of $\delta^2\text{H}_c$ were repeatable for males but not for females, suggesting that winter-site fidelity could differ between sexes. The data presented here emphasize the importance of tracking migratory populations across multiple years to uncover factors affecting population dynamics.

Keywords: Deuterium, stable isotopes, repeatability, migration, geolocator, songbird

Introduction

Migratory animals use multiple habitats during the annual cycle, generally including separate locations for breeding, wintering, and migratory stopover. Site fidelity, or the degree to which an individual returns to the same locations in subsequent years, can have profound effects on individual fitness, population viability, and movement of disease (Møller and Szép 2011). Whereas breeding philopatry (i.e., returning to the same breeding location) has been studied extensively (Bensch et al. 1998; Winkler et al. 2004; Brown, Roche, and Brown 2017), wintering fidelity has received less attention (Robertson and Cooke 1999). This is surprising, given the fact that many birds spend more time on wintering grounds than at all other sites combined (La Sorte et al. 2017). In light of this, the bias favouring studies on the breeding grounds is clear and it is assumed that advancement in technology and analytical tools will reverse such bias (Marra et al. 2015). Understanding how faithful individual migrants are to wintering sites is an important consideration for both basic population biology and more applied conservation studies of migratory birds.

Returning to the same wintering location over multiple years may benefit individuals in several ways. First, familiarity with a local area may enhance access to the best-quality habitat and resources (local knowledge hypothesis; Rohwer and Anderson 1998). Not only does winter habitat quality affect overwinter survival, but carryover effects may also influence reproductive success during the subsequent breeding season (Norris et al. 2003; Norris et al. 2004; Saino et al. 2004; Rockwell et al. 2012; Rushing et al. 2016). Second, in species that reunite with breeding partners during winter, wintering site fidelity can serve an important social function (as in Common Eiders, *Somateria mollissima*, Spurr and Milne 1976; Barrow's Goldeneye, *Bucephala islandica*, Savard 1985; Harlequin Ducks, *Histionicus histrionicus*, Gowans et al. 1997). Third,

prior exposure to the local parasite communities, and the immunological advantage this may
60 confer, has been proposed to favor fidelity to both breeding and wintering sites (Møller and Szép
2011). However, site fidelity to wintering grounds may be disadvantageous if site-faithful
species are unable to respond flexibly to annual variation in winter conditions or anthropogenic
disturbance (La Sorte et al. 2017). Thus, the relative costs and benefits of winter-site fidelity vary
across species.

65 Stable isotope analysis (Hobson and Wassenaar 1997) provides a means of examining
population or individual approximate origins by taking advantage of geographic variation in
food-web isotopic values. Stable isotope values of metabolically inert tissues such as keratinous
feathers or claws reflect the local food webs in which these tissues were formed and can thus
provide geographic information on the subject's prior locations, especially for stable hydrogen
70 isotope values ($\delta^2\text{H}$; Hobson 2008). For species that undergo a prealternate molt (i.e., before
spring migration), feathers are an ideal tissue to assess wintering latitude of birds captured at
stopover or breeding grounds (Hobson and Wassenaar 1997; see Yohannes et al. 2008).
However, not all species molt at the appropriate time to use feathers to track winter origins. In
North America, most migratory songbirds complete their pre-basic molt before migration from
75 the breeding grounds and often lack a pre-alternate molt (Pyle 1997). For these species, stable
isotope analysis of claw tissue collected upon arrival to the breeding ground offers a promising
alternative to feather samples (Mazerolle and Hobson 2005; Fraser et al. 2008; Hopkins, Cutting,
and Warren 2013).

In this study, our objective was to assess whether Song Sparrows (*Melospiza melodia*) are
80 consistent in winter site fidelity within age and sex classes, and to assess whether winter site use
is affected by annual variation in winter climate. We assessed winter-site fidelity using claw $\delta^2\text{H}$

values ($\delta^2\text{H}_c$) of winter-grown claw tissue collected in spring at their breeding site over six years. We hypothesized that Song Sparrows are consistent across years in returning to the same wintering sites, regardless of variation in climate (average winter temperature and precipitation).
85 If this is true, we predict that birds captured in multiple years would have consistent and significantly repeatable $\delta^2\text{H}_c$ values. Alternatively, it is possible that individual birds are consistent in relative migration distance, but do not exhibit strict winter site fidelity. In that case, we predict that Song Sparrows captured in multiple years would have significantly repeatable $\delta^2\text{H}_c$, but that $\delta^2\text{H}_c$ values would vary across year in relation to winter climate. To test these
90 predictions, we examined variation and repeatability in latitudinal migration distance within individuals, among years, between the sexes, and between age classes. Additionally, we confirmed the reliability of inferring winter location from claw $\delta^2\text{H}$ by equipping a subset of individuals with geolocators prior to fall migration, retrieving them the following spring, and compared geolocator-derived wintering latitudes to $\delta^2\text{H}_c$ values. This extensive six-year dataset
95 examining repeated samples permits a more robust analysis than our previous analysis of only two winters (Kelly et al. 2016), in addition to validating isotopic data with geolocator data.

Methods and Materials

Study population and field methods

We captured Song Sparrows breeding at a long-term study site near Newboro, Ontario
100 (44.66 °N/76.22 °W) on land owned by the Queen's University Biological Station. This population has been studied for over 15 years, thus age and breeding history is known for most individuals and standard field methods have been established. Field work was conducted during April and the first week of May 2012 through 2017 (Table 1). We captured birds in seed-baited Potter traps, which we checked each hour between 06:30 h and 10:30 h. We determined sex

105 based on the presence (male) or absence (female) of a cloacal protuberance, the presence of a
brood patch (incubating female), supplemented by measurements of unflattened wing chord,
measured to the nearest 0.1 mm using dial calipers. We outfitted birds with a Canadian Wildlife
Service aluminum band for individual identification. We inferred age from previous years'
capture and banding records and considered previously unbanded adults to be one year of age (in
110 their second year = SY; after second year = ASY) at first capture (Lapierre et al. 2011). Before
release, we clipped a small sample of claw tissue (approx. 2.5 mm; Figure 1) from the distal
portion of each hallux claw for stable isotope analysis. Animal procedures were approved by the
Animal Use Subcommittee of Western University (protocols 2008-054 and 2016-017) and
federal approval from Environment and Climate Change Canada (permit 10691).

115 *Stable isotope analysis*

We soaked, agitated and rinsed claw samples in 1.6 mL of 2:1 chloroform-methanol
solution to remove any dirt or oils that might contaminate isotope analyses. We removed excess
chloroform-methanol and dried claw samples overnight in a fume hood. Samples were stored at
room temperature in a sterile 96-well microplate for two weeks to equilibrate to lab conditions.
120 Once dry, we weighed nails to $350 \mu\text{g} \pm 10 \mu\text{g}$ (Mettler Toledo MX5 Microbalance PSU30A-3)
and crushed samples in silver capsules.

We analyzed samples for $\delta^2\text{H}$ for the period 2012 – 2015 at the Stable Isotope Laboratory
of Environment Canada, Saskatoon, Canada, and 2016 and 2017 at Western University's LSIS-
AFAR isotope lab. In each laboratory we derived $\delta^2\text{H}$ values for the nonexchangeable hydrogen
125 portion of claws using online continuous-flow isotope mass spectrometry (CF-IRMS). In
Saskatoon, we combusted samples at 1350 °C using pyrolytic (glassy carbon) combustion in a
Hekatek furnace interfaced with a Micromass Isoprime mass spectrometer (Micro-mass UK,

Manchester, UK). At the LSIS-AFAR laboratory, we combusted samples at 1020 °C using a Chromium-based reactor in a Flash Elemental Analyser interfaced with a Thermo Delta V Plus isotope ratio mass spectrometer (Thermo Instruments, Bremen, Germany). At both laboratories, we corrected the influence of exchangeable hydrogen by performing $\delta^2\text{H}$ analyses using the comparative equilibrium method using two keratin standards (Caribou Hoof Standard [CBS]: -197 ‰, and Kudu Horn Standard [KHS]: -54.1 ‰; Wassenaar and Hobson, 2004). All keratin $\delta^2\text{H}$ results are reported in units of per mil (‰) and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale. Based on within-run replicate analyses of each keratin standard the analytical precision is estimated to be ± 2 ‰.

Depicting likely winter locations of Song Sparrows from $\delta^2\text{H}_c$

We created a probabilistic surface of potential wintering origins for our Song Sparrows breeding near Newboro, ON using procedures outlined in Hobson et al. (2014). We used an algorithm derived from warblers and thrushes ($\delta^2\text{H}_f = 24.1 + 1.3 (\delta^2\text{H}_c)$; Hobson, unpublished data) to convert our $\delta^2\text{H}_c$ values to $\delta^2\text{H}_f$ -equivalents since no isoscape based on $\delta^2\text{H}_c$ yet exists. We then combined calibrated $\delta^2\text{H}_c$ values with a model of expected $\delta^2\text{H}_f$ values to establish a $\delta^2\text{H}_c$ isoscape formed using amount-weighted growing season average precipitation ($\delta^2\text{H}_p$) data from the Global Network of Isotopes in Precipitation (GNIP) and restricting the geographic range of potential sites to eastern North America, including the known range of Eastern Song Sparrows. A raster surface of expected $\delta^2\text{H}_c$ values was based on the calibration algorithm $\delta^2\text{H}_f = -36.9 + 0.95 * \delta^2\text{H}_p$ for ground-foraging short-distance migrants (Hobson et al. 2012). We defined possible origins as being the entire eastern range of the Song Sparrow in North America and arbitrarily delineated the western boundary to correspond approximately to the distribution of the

eastern Song Sparrow since western subspecies of Song Sparrows remain resident year-round (Patten and Pruett 2009). Furthermore, our study population has had two individuals captured at banding stations in Maryland and Tennessee during the winter, suggesting a primarily southward migration. Following the general approach of Hobson et al. (2014), we derived a spatially-
155 explicit probability density surface depicting potential wintering origins for each individual Song Sparrow using the likelihood that a claw (based on feather equivalent $\delta^2\text{H}$ values) originated at each pixel (Royle and Rubenstein 2004). We included error (18.4 ‰) corresponding to the standard deviation of the residuals in the calibration algorithm linking feather and precipitation $\delta^2\text{H}$. We then identified the set of spatial coordinates defining the upper 33 % of the cumulative
160 density function and coded those as 1 (high probability of winter occurrence), with all others as 0 (low probability of winter occurrence). We combined these geographically indexed densities into a single surface to describe the potential origins of all 301 individual Song Sparrows, for males and females separately, as well as for winters that were significantly different from others as determined via model selection.

165 *Geolocator analysis*

In late August and September 2014 and mid-July 2015, we attached light-level geolocators (MK6 Series, Biotrack) to 32 (13 SY and 19 ASY) male Song Sparrows, prior to fall migration to determine their subsequent wintering locations. Table 2 summarizes geolocator releases for the two years. We constructed harnesses with two 38 – 41 mm leg loops (Rappole and Tipton 1991) using plastic rubber cord (~ 2 mm diameter). The combined weight of the
170 geolocator and harness was 0.39 – 1.0 g, less than 5 % of the average body mass for this study population (mean \pm SEM = 22.6 g \pm 0.14 g).

We retrieved geolocators upon recapturing birds the following April (i.e., April 2015 and 2016, for geolocators deployed in 2014 and 2015, respectively; n = 9 devices retrieved; Table 2).

175 We analyzed the light data stored on geolocators with the BASTrak software package (Fox 2008), employing the threshold method of analysis. We corrected errors in clock drift with BASTrak's Decompressor. Sunrise and sunset times were estimated in TransEdit2, using a threshold of five arbitrary light units. False transitions, due to shading during daylight hours, and unreliable estimates, due to proximity to the solar equinox, were identified using minimum dark

180 period (six hours) and equinox filters (within three weeks of the equinox), respectively. Any remaining false transitions were flagged manually. False transitions were deleted, and equinox data were excluded from positional estimates (though not from sun angle calibrations). We assessed sunrise and sunset events individually, gave high confidence values to transitions with smooth curves and retained such transitions in the analysis. There were many unanticipated

185 shading events during sunrise and sunset, making it difficult to determine, with absolute certainty, true sunrises and sunsets. We thus retained only uninterrupted sunrise and sunset transitions, resulting in a limited number of wintering-grounds estimates. See Supplementary Material for an example of excluded unfiltered positions (Figure S1).

We previously determined that the distal 2.5 mm of hallux claw tissue corresponds to

190 tissue grown at the wintering grounds (approx. end November – February; Kelly et al. 2016). Corresponding to this time window, we considered light data from December – February for wintering locations (mean = 10.5 ± 1.32 days). We used individual sun elevation angles for each Song Sparrow (DSKY = -3.25; DWYS = -2.0; ROYS = -3.2; DKDS = -2.0; DRDS = -2.5; DWOS = -3.0; DYDS = -2.4; MRYS = -2.7). These were calculated using the Hill-Ekstrom

195 calibration method (Lisovski et al. 2012; Ekstrom 2004; Hill and Braun 2001). Longitudinal

shifts suggested the birds were exiting their stationary winter period at, or just after, the spring equinox. The uncertainty in latitudinal data around the equinox creates the greatest variance in location estimates, and thus the greatest resolution for the Hill-Ekstrom method. All calibrations were done with smooth transitions from the three weeks leading up to the spring equinox. We include additional approaches to calculating the sun elevation angle in the Supplementary Material.

We assessed the error associated with the geolocator-obtained Song Sparrow locations by contrasting sunrise and sunset-derived locations from the light data during the breeding season with the geographic position of their breeding site (July – August). This error was averaged across comparisons and estimated to be ± 211 km for estimations of latitude and ± 65 km for longitude from geolocators released in 2015. Releases in 2014 were too late in the season (late August and September) to guarantee the bird remained on the breeding grounds and estimates are thus unreliable.

Statistical analyses

We used an information theoretic approach (Burnham and Anderson 2002) and Akaike's information criterion corrected for small sample sizes (AICc) to compare support for 17 alternative models predicting $\delta^2\text{H}_c$. We used linear mixed models, constructed with *lmer* in the R package lme4 (Bates et al. 2015), to identify predictors of $\delta^2\text{H}_c$. All candidate models included bird ID as a random effect. Models differed in the presence versus absence of the following fixed effect predictors of $\delta^2\text{H}_c$: age class (i.e., SY or ASY), sex, year, plus all second-order interactions (sex x age, year x sex, year x age; Table 3). The candidate model set also included a null model, i.e., $\delta^2\text{H}_c \sim 1$. We compiled model-averaged parameter estimates from the full set of AICc-ranked

candidate models using the conditional averaging method (Burnham and Anderson 2002) implemented in *model.avg* in the R package MuMIn (Bartoń 2016).

220 We used the same statistical approach described above to compare support for 13 alternative models predicting $\delta^2\text{H}_c$, with reference to climatic variables. We averaged the temperature and precipitation, respectively, in the months of December, January, and February for the South-eastern United States as indicators of winter climate (NOAA 2018). We could not combine these variables with the former analysis since the average temperature and precipitation
225 values are confounded with year. All candidate models included bird ID as a random effect. Models differed in the presence versus absence of the following fixed effect predictors of $\delta^2\text{H}_c$: sex, average temperature, average precipitation, plus all second-order interactions (sex x average temperature, sex x average precipitation, average temperature x average precipitation).

We calculated repeatability of $\delta^2\text{H}_c$ using two methods: based on among- and within-
230 individual components of variance derived (1) from a one-way ANOVA (Lessels and Boag 1987) and (2) from linear mixed effects models (LMMs; Nakagawa and Schielzeth 2010) on the 92 birds from which claw tissue had been sampled in multiple years. We examined repeatability for the entire dataset and separately for each sex (males, $n = 63$; females, $n = 29$; Table 3). While the ANOVA compared variances considering only the individuals, the LMMs included a random
235 intercept of individual ID as well as year and age as main effects for sex-specific investigations. Sex was included as a main effect in addition to year and age in the model estimating repeatability for the entire population. To confirm significance of LMM-estimated repeatability, we considered the difference in log-likelihood values compared against χ^2 critical value of one degree of freedom (Nakagawa and Schielzeth 2010; see Supplementary Material for detailed
240 analysis).

To investigate how predictions of winter origin based on $\delta^2\text{H}_c$ agreed with geolocator results, we used a linear regression (lm, implemented in base R version 3.4.1; R Core Team, 2017) to relate $\delta^2\text{H}_c$ to corresponding latitudes obtained from geolocators. We coded $\delta^2\text{H}_c$ as the independent variable and the average geolocator-derived latitude, of all useable days for each
245 bird, as the dependent variable.

Results

Of the candidate models predicting $\delta^2\text{H}_c$, the best supported model included effects of sex, year, and their interaction (Table 3). Models including effects of year and sex were ranked higher than those without. Female Song Sparrows had less negative $\delta^2\text{H}_c$ values than males
250 ($F_{1,581}=3.72$, $p = 0.01$; female = -66.1 ± 1.1 ‰ [mean \pm SEM], male = -69.0 ± 0.9 ‰), indicating that females overwintered farther south, on average, than males (Figure 2; Figure 3). We also observed a significant interaction of sex and year, indicating that the magnitude of the sex difference in latitudinal migration distance varied across years. Specifically, the average overwinter latitude calculated for females in the winter of 2014-2015 was significantly farther
255 south than that calculated for females in the winter of 2011-2012 (Table 5; Figure 2). Values of $\delta^2\text{H}_c$ were generally consistent among years, except for winter 2015–2016 (Figure 4; Figure 5; visualized in Supplementary Figure S2).

Of the candidate models predicting $\delta^2\text{H}_c$ in relation to climate, the best supported model included sex, average precipitation, and their interaction (Supplementary Table S1). Models
260 including sex and average precipitation ranked higher than those without. Winters with more precipitation were associated with more negative $\delta^2\text{H}_c$ values (Supplementary Table S2).

Over the six years of this study, we captured 301 unique Song Sparrows and collected 449 claw samples. Among the 92 individuals that were sampled over multiple years (Table 4), $\delta^2\text{H}_c$ values were repeatable for both methods (ANOVA repeatability = 0.083, $F_{91,133} = 1.53$, $p = 0.012$; LMM repeatability = 0.032, $p < 0.05$) when pooling both sexes. When calculating repeatability for males and females separately, $\delta^2\text{H}_c$ values were repeatable for males using both methods (ANOVA repeatability = 0.084, $F_{66,99} = 1.56$, $p = 0.021$; LMM repeatability = 0.070, $p < 0.05$). Females had significant repeatability using the LMM method, albeit a low repeatability value (repeatability = 0.0008, $p < 0.05$), but repeatability was not significant using the ANOVA method (repeatability = 0.10, $F_{31,27} = 1.43$, $p = 0.17$). Detailed calculations of LMM repeatability is reported in Supplementary Material.

Three of the sixteen geolocators deployed in 2014 and six of the sixteen geolocators deployed in 2015 were retrieved, one of which did not have usable data. Thus, we had usable data on wintering locations for a total of eight geolocators (Table 2). Values of $\delta^2\text{H}_c$ were negatively associated with latitudes determined from geolocators, albeit not significantly ($R^2 = -0.476$, $F_{1,6} = 5.35$, $p = 0.06$; Figure 6). Additional approaches to calculating the sun elevation angle and their respective correlations with $\delta^2\text{H}_c$ values are reported in Supplementary Material (Table S3; Figure S3). All approaches yielded the same relationship, suggesting consistent relative wintering latitude estimates between isotope and geocator based methods.

Our assignments reveal that this breeding population of Song Sparrows likely winters south of the Great Lakes and that their wintering range extends southward to the Coastal Plains while avoiding the Appalachian Mountains (Figure 1). Wintering locations of males and females in this population likely overlap, but samples from males were assigned to higher latitudes, on average, than those of females (Figure 3). Assignments also reveal that the likely wintering

285 locations during 2015 – 2016 were at higher latitudes than for other years (Figure 5), with a deficit of assignments in Louisiana and Florida for that winter. Assignments for each year are included as Supplementary Material (Figure S2).

Discussion

We present the largest dataset of tissue $\delta^2\text{H}$ values corresponding to wintering origins for a North American songbird population. Our six-year dataset of $\delta^2\text{H}_c$ values, validated by comparison with geolocator estimates of overwinter locations, is generally consistent with that of Kelly et al. (2016) and our prediction that individual Song Sparrows are consistent (repeatable) in their migration to wintering grounds. However, the overall pattern of repeatability is driven primarily by males. Our findings presented here and earlier (Lymburner et al. 2016) confirm that females overwinter farther south than males but also reveal that the magnitude of sex differences in overwinter latitude varied annually. We thus conclude that Song Sparrows are consistent in relative migration distance, but that there is sex-specific year to year variation in wintering site use.

Long-term datasets of large-scale geographic movement data for animals are rare, mainly due to logistical challenges and equipment costs. We provide evidence that $\delta^2\text{H}_c$ is a reliable method to track the origins of migratory Song Sparrows, particularly for studies focusing on relative (latitudinal) migration distances such as within-population analyses in North America. Most feathers are only replaced during regular molt periods, but claws grow continuously throughout the year. Claw may thus be used as an alternative to feathers when using $\delta^2\text{H}$ to track migratory origins of birds (see White-throated Sparrow *Zonotrichia albicollis*, Mazerolle and Hobson 2005; Golden-winged Warbler *Vermivora chrysoptera* and Cerulean Warbler *Setophaga cerulea*, Fraser et al. 2008; White-ruffed Manakin *Corapipo altera*, Boyle et al. 2011; Snow

Bunting *Plectrophenax nivalis*, Macdonald et al. 2013), critical for many breeding North American birds that lack a prealternate molt. It is important to note that we studied a ground-
310 foraging species and differences in claw growth among avian life-histories may affect the period over which claw tissue data are appropriate (Bearhop et al. 2003). Using techniques in combination will allow a more comprehensive examination of the question and allow testing of multiple hypotheses concurrently (see Contina et al. 2013; Pérez et al. 2014).

We sought to validate our $\delta^2\text{H}_c$ analyses with geolocator data. Our ability to do so was
315 limited by the number of recovered loggers, and by the noisy data from those recovered. A high frequency of shading events resulted in nonsensical position estimates (Supplementary Figure S1), so we used stringent criteria to include only clean transitions in light levels, but this substantially reduced sample size. We also evaluated the relationship between $\delta^2\text{H}_c$ and geolocator-derived latitudes using three different estimations of the sun elevation angle
320 (Supplementary Material Table S3), as well as using all geolocator-derived positions in addition to their average (Supplementary Material, Figure S3). Regardless of methodology, the relationships between $\delta^2\text{H}_c$ and geolocator-derived latitudes was evident ($R^2 = 0.315 - 0.476$ across six analyses; Supplementary Material Figure S3).

At the population level, the distribution of wintering latitudes indicated by $\delta^2\text{H}_c$ values
325 was generally consistent between years, with only one year (2015 – 2016 winter) characterized by unusually negative $\delta^2\text{H}_c$ values. A strong El Niño event that winter resulted in the highest recorded average temperatures for December through February in the United States (NOAA 2016). These warm temperatures may explain the northerly winter latitudes and short migration distances inferred for that year. However, winter temperature was not a significant predictor of
330 $\delta^2\text{H}_c$ and precipitation was more closely associated with $\delta^2\text{H}_c$. The extent to which highly

negative $\delta^2\text{H}_c$ values in 2015-2016 reflect more northerly wintering locations of Song Sparrows as opposed to the amount effect (Clark and Fritz 1997) remains unclear (Welker 2012; Liu et al. 2013).

Male Song Sparrows return to the breeding grounds earlier in spring than females in our
335 study population (Lymburner et al. 2016). Wintering latitude contributes to this pattern of
protandry, in that males overwinter farther north (closer to the breeding grounds) than do
females, on average. Similar patterns of sex-specific wintering latitudes have been documented
for many species (see Komar et al. 2005) and sex differences in overwintering latitude have been
suggested as a proximate mechanism of protandry (Schmaljohann et al. 2015). Our findings
340 support this hypothesis, although other mechanisms such as sex differences in flight speed or
departure dates may also contribute. Our large sample size (males, $n = 271$; females, $n = 172$)
and residual error (18.4 %) resulted in spatial assignments at the population level covering broad
wintering areas. Sources of residual error may include variation in $\delta^2\text{H}_c$ expected from altitudinal
differences across individual song sparrows and their relative proximity to the ocean (Hobson
345 2008). However, this approach allows the analysis of large sample sizes, can be used to get a
relative understanding of behavioral differences among sex and age classes, and can be
constructively combined with other tools to better define fidelity.

Male Song Sparrows had significantly repeatable $\delta^2\text{H}_c$ values: this suggests that males
may return to the same general wintering locations in consecutive years. Previous studies of
350 winter-site fidelity in other species either did not address sex differences (Turnstones *Arenaria*
interpres and Purple Sandpiper *Calidris maritima*, Burton and Evans 1997) or reported equal
fidelity of sexes to wintering sites (Prairie Warbler *Dendroica discolor*, Latta and Faaborg
2011; Sanderlings *Calidris alba*, Lourenco et al. 2016), making this study the first to our

knowledge that reports sex differences in winter-site fidelity. However, it is possible that our
355 inconsistent significance of female $\delta^2\text{H}_c$ repeatability may be due to sex differences in return
rate, resulting in sex differences in sample size and statistical power. Alternatively, the optimal
balance between site fidelity versus flexibility in wintering locations may differ between the
sexes resulting in sex-specific winter-site fidelity. First, the larger body size of male Song
Sparrows (Arcese et al. 2002) may permit greater tolerance of temperature fluctuations resulting
360 in greater winter-site fidelity. Second, territory defence by male Song Sparrows outside of the
breeding season (Arcese 1987; Wingfield 1994) may also increase male winter-site fidelity. At a
larger spatial scale, the fact that parasite communities vary geographically (Pagenkopp et al.
2008; Merino et al. 2008; Clark, Clegg, and Klaassen 2016) suggests that returning each winter
to the same general latitude may limit the diversity of pathogens encountered and favor site
365 fidelity to wintering areas (Møller and Szép 2011). Considering this and evidence that males may
have lower immunocompetence and greater susceptibility to parasites than females (McCurdy et
al. 1998; Møller, Corci, and Erritzøe 1998), winter-site fidelity may be more beneficial to males
than females.

In conclusion, returning to similar ecological habitats in consecutive years should confer
370 fitness benefits if familiarity increases access to resources (Rohwer and Anderson 1988) and
local adaptation to the pathogen community (Møller and Szép 2011). However, the spatial
resolution of our isotope data does not permit drawing conclusions about fine-scale site fidelity
during winter. Further testing the hypothesis that males have greater fidelity to specific wintering
sites than females will require further studies with methods that allow tracking of space use over
375 the winter with high spatial resolution.

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